

TAXONOMY OF THE *CUSCUTA SALINA-CALIFORNICA* COMPLEX (CONVOLVULACEAE)

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ABSTRACT

The *Cuscuta californica* complex (*Cuscuta* subsect. *Californicae*) is recircumscribed to include the species from subsect. *Subinclusae*. The species include *C. salina*, *C. susksdorfii*, *C. californica*, *C. occidentalis*, *C. subinclusa*, and *C. howelliana*. A summary of relevant taxonomic information is provided, along with a key to species and varieties, synonymy, distribution, host range, and conservation status. Morphology and micromorphology of flowers, seeds, and capsules are analyzed and illustrated.

RESUMEN

El complejo *Cuscuta californica* (*Cuscuta* subsect. *Californicae*) está circunscrito a incluir las especies de subsect. *Subinclusae*. Las especies incluyen *C. salina*, *C. susksdorfii*, *C. californica*, *C. occidentalis*, *C. subinclusa*, y *C. howelliana*. En este trabajo se presenta un resumen de la información taxonómica junto con una clave para identificar las especies y variedades, sinónimos, distribución, variabilidad de huéspedes y estado de conservación. Se analizan e ilustran la morfología y micromorfología de las flores, de las semillas y de las cápsulas.

Yuncker (1932) described and defined *Cuscuta* subsect. *Californicae* and subsect. *Subinclusae* mainly on the basis of absence or presence, respectively, of infrastaminal scales. He suggested that both sections were derived independently but in parallel from subsect. *Arvenses*. In Yuncker's view, subsect. *Californicae* comprised five species: *C. californica* Hook. & Arn., *C. occidentalis* Millsp., *C. brachycalyx* Yuncker, *C. jepsonii* Yuncker, and *C. sandwichiana* Choisy, while subsect. *Subinclusae* included three species: *C. salina* Engelm., *C. susksdorfii* Yuncker, and *C. subinclusa* Durand & Hilgard (Yuncker 1932, 1965). *Cuscuta howelliana* Rubtzoff was recently described (Rubtzoff 1966) and noted by its author to have similarities to *C. susksdorfii* of subsect. *Subinclusae*.

Definitions and interrelationships among these taxa are complex. Beliz (1993) included *Cuscuta brachycalyx*, *C. occidentalis*, and *C. suksdorfii* as synonyms of *C. californica* var. *breviflora* Engelm. *Cuscuta subinclusa* and *C. howelliana* were hypothesized to be sister species in a separate clade (Beliz 1986). Some taxa were described in one subsection and later were reclassified in the other. For example, Engelmann (1859) initially described *C. salina* as “?*C. californica* var. *squamigera*” and as *C. subinclusa* var. *abbreviata* (see also the example below of *C. suksdorfii*). *Cuscuta sandwichiana* (Beliz 1986; Costea et al. 2006a) and *C. jepsonii* (Beliz 1986; Costea et al. 2006c) do not appear to be evolutionarily related to this group.

Circumscriptions of these taxa and an assessment of their relationships are provided here on the basis of the morphology and micromorphology of flowers, capsules, seeds, and pollen. Conservation status is assessed for all taxa.

METHODS

Descriptions of morphology (see Costea et al. 2006a) are based on samples from specimens of the NY, JEPS, and UC herbaria (Appendix 1). Measurements and pictures were taken with a scanning electron microscope Hitachi S-570 at 15 KV. Samples were coated with 30 nm gold using an Emitech K 550 sputter coater. Conservation status was determined using NatureServe (2005) ranks and criteria.

TAXONOMY

Delimitation of the *Cuscuta salina-californica* complex

Our observations suggest that the species of subsections *Californicae* and *Subinclusae* form a single phylogenetic group. We hypothesize that infrastaminal scales have undergone a gradual reduction from fimbriate scales or ridges in *C. salina*, to dentate wings in *C. suksdorfii*, to complete reduction in *C. californica* and *C. occidentalis*. A similar reduction of infrastaminal scales has occurred in *C. indecora* complex (subsect. *Indecorae* Yuncker) (Costea et al. 2006c). *Cuscuta subinclusa* and *C. howelliana* have well-developed infrastaminal scales and were suggested by Beliz (1986) to form a distinct clade in which a cylindrical-campanulate corolla has evolved as a specialization to butterfly pollination. Although *C. subinclusa* and *C. howelliana* are distinct in their microreticulate pollen (see descriptions below), close similarities in morphology and micromorphology of calyx, corolla lobes, seeds, and capsules (see below) indicate that they probably belong to the same phylogenetic group as *C. californica*, *C. salina*, and *C. suksdorfii*. A cylindrical-campanulate corolla sometimes occurs in *C. californica*, and Engelmann (1876) noted that “in many respects [*C. salina*] is intermediate between the preceding [*C. californica*] and the following species [*C. subinclusa*].” Yuncker (1932, 1965) observed that the corolla of *C. subinclusa* is “usually showing horizontal ridges between the stamen at-

tachments” and we find this characteristic in some flowers of *C. californica* as well. The original description of *C. howelliana* (Rubtzoff 1966) noted that it is similar to *C. suksdorfii* var. *subpedicellata*.

Cuscuta jepsonii and *C. sandwichiana* were included by Yuncker (1932) in subsect. *Californicae* (the latter species omitted in the treatment from 1965) because they exhibit a similar reduction of the infrastaminal scales. *Cuscuta jepsonii*, however, may be evolutionarily related to taxa of *Cuscuta indecora* complex (Costea et al. 2006c). *Cuscuta sandwichiana* is a Hawaiian endemic and was hypothesized by Costea et al. (2006a) to belong to the *C. pentagona* complex.

In conclusion, the *Cuscuta salina-californica* complex in our view includes *C. salina*, *C. susksdorfii*, *C. californica*, *C. occidentalis*, *C. subinclusa*, and *C. howelliana*, which are recognized here as *Cuscuta* subsect. *Californicae* Yuncker (including subsect. *Subinclusae*). Taxonomically and nomenclaturally problematic species are discussed below.

***Cuscuta subinclusa*.**—Curran (1885) noted that “from the description, [*C. ceanothi* is] evidently *C. subinclusa*,” and the former name has been used by most authors (e.g. Yuncker 1965) because it has priority. From Curran’s observation it can be inferred that the type collection of *C. ceanothi* was not available even at 1885. This collection may have been destroyed during the fire following the San Francisco earthquake from 1906 or even at an earlier date. As observed by Beliz (1986), it is possible that the name *C. ceanothi* refers to a species distinct from *C. subinclusa*. The protologue of *C. ceanothi* states that flowers are urceolate with obtuse calyx lobes, features not encountered in *C. subinclusa* or in any species hypothesized to be closely related. In a letter addressed to Engelmann on 10 Nov 1860 (Ertter 2003), Behr wrote: “Of *Cuscuta* I know two kinds, the one quite common on *Salicornia* (*C. salina*?), the other climbs on *Ceanothus*. Of the latter I gave once a diagnosis in the transactions (Proc. Calif.) under the preliminary name *Cuscuta ceanothi*. This diagnosis is by the nature of a search very incomplete, as for comparison I had only the just-mentioned parasitic kind on the *Salicornia* and none of the more closely related exotics.” In a summary of the San Francisco flora (1888), approximately three decades after describing *C. ceanothi*, Behr mentioned *C. subinclusa* but not *C. ceanothi*. Without neotypification, there apparently is no way to establish the identity of *C. ceanothi*, and until more certainty might exist that *C. ceanothi* is not a distinct and evidently rare species, we use the later name *C. subinclusa* for the known species.

***Cuscuta suksdorfii*.**—Yuncker (1921) described *C. salina* var. *acuminata* Yuncker, which he later (1932) treated at specific rank as *C. suksdorfii*. This species is “closely allied with *C. salina*” from which it differs in the morphology of calyx and corolla, infrastaminal scales reduced to dentate wings, and multiseeded

capsules. Beliz (1986) originally treated *C. suksdorfii* as a variety of *C. salina*, but later (1993) she included it as a synonym of *C. californica* var. *breviflora*, together with *C. occidentalis* and *C. brachycalyx*. Indeed, *C. suksdorfii* shares some characteristics with both *C. salina* (e.g., presence of infrastaminal scales as well as seed and pollen morphology—see descriptions) and *C. californica*/*C. occidentalis* (e.g., multiseeded capsules), but we consider that treating it at specific rank better represents the differences in morphology and biology as well as the evolutionary relationships between all the taxa involved (see below). *Cuscuta suksdorfii* var. *subpedicellata* Yuncker with flowers sessile or subsessile, shorter calyx (1.6–2 mm long) and capsule globose to depressed globose, is treated formally at varietal rank.

***Cuscuta californica* and *C. occidentalis*.**—By describing *C. brachycalyx*, Yuncker (1932, 1965) obscured the already tenuous distinction between *C. californica* and *C. occidentalis*. Although homotypic, *C. californica* var. *brachycalyx* Yuncker and *C. brachycalyx* have slightly different protologues. *Cuscuta californica* var. *brachycalyx* has “corolla campanulate, lobes ... shorter than the tube ...” (Yuncker 1921, p. 62); *C. brachycalyx* has “corolla campanulate-globose, saccate between the stamen attachments, lobes ... shorter than or about equaling the tube” (Yuncker 1932, p. 159) and “is closely related to *C. californica*, but differs by its very short calyx and more obtuse perianth lobes.” Yuncker did not mention the saccate corolla that would separate *C. brachycalyx* from *C. californica* but that would bring it close to *C. occidentalis*. Not surprisingly, Beliz (1986) concluded that “all names proposed for the numerous perianth and anther size variants within *C. californica* do not warrant taxonomic recognition ...,” and she included both *C. occidentalis* and *C. brachycalyx* as synonyms of *C. californica* var. *breviflora* (Beliz 1986, 1993). We find that indeed two different major entities, corresponding to *C. californica* and *C. occidentalis*, can be distinguished in most cases, based on a combination of characters. Plants called *C. brachycalyx* by Yuncker, with a short calyx and a long (ca. 2.5 mm) campanulate corolla tube that may become somewhat saccate in fruit, possess all the characteristics of *C. californica* (see below). Although such plants are occasionally distinct, at other times the calyx/corolla tube ratio may vary even on the same plant, from flowers with calyx ca. equaling the corolla tube to flowers with calyx ca. 1/2 of the corolla tube length (Fig. 1 a, b, c). Apparently the corolla tube may continue to grow from the beginning of anthesis until fructification, significantly altering the ratio between calyx and corolla tube lengths. Similar infraspecific variation of the ratio between calyx and corolla tube lengths may be encountered in *C. gronovii* (between var. *gronovii* and var. *latiflora* Engelm.), but here the entities are relatively discrete (Costea et al. 2006b). For these reasons, *C. brachycalyx* is here considered conspecific with *C. californica* and not recognized at any rank.

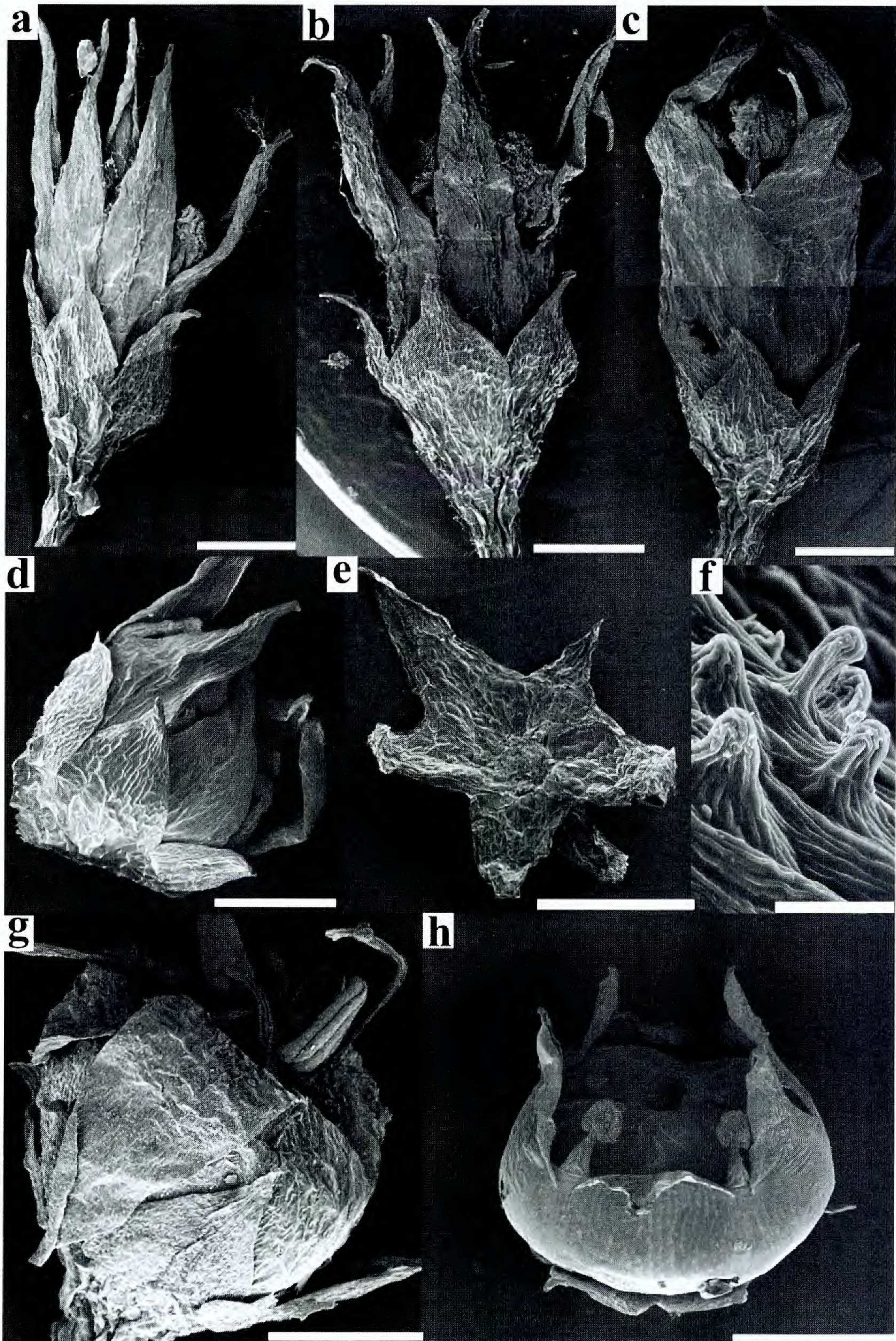


FIG. 1. Morphology of flowers and capsules. **a–c.** *Cuscuta californica* var. *californica*. Variation of corolla tube length in flowers of the same individual (scale bar = 1 mm). **d.** *C. occidentalis*—flower (scale bar = 1 mm). **e.** *C. suksdorfii*—calyx (scale bar = 0.75 mm). **f.** Papillae on corolla of *C. howelliana* (scale bar = 7 μ m). **g–h.** Capsules surrounded by corolla: **g.** *C. californica*, **h.** *C. occidentalis* (scale bar = 1 mm).

Some plants of this complex produce a short (1.5–2 mm), campanulate-globose corolla tube (as in *Cuscuta occidentalis*) and long anthers/styles (as in *C. californica*), or plants may show reversed character states (corolla tube long and campanulate and anthers/styles short). Such intermediate-like plants occur at a frequency of ca. 1–2% of specimens examined. It is unclear if they are result of hybridization, which has never been clearly documented in *Cuscuta*, or evidence of variation in closely related and incompletely differentiated taxa. Because such possibly intermediate plants are relatively few, and to avoid nomenclatural changes, we maintain *C. californica* and *C. occidentalis* as distinct species. Several varieties within *C. californica* usually can be distinguished, based on single characters. *Cuscuta occidentalis* is less variable; a few collections were found to possess papillose flowers like *C. californica* var. *papillosa*, but the origin of this variation is unclear.

KEY TO SPECIES OF THE *CUSCUTA SALINA*-*CALIFORNICA* COMPLEX

1. Infrastaminal scales present (sometimes reduced to ridges), fimbriate.
 2. Flowers 5–7(–9) mm long; calyx ca. 1/2 of the corolla tube, with lobes overlapping at base; corolla lobes 1/4–1/3 as long as the tube; anthers 0.8–2 mm long _____ **3. *C. subinclusa***
 2. Flowers 2.8–5(–6.) mm long; calyx ca. equaling or somewhat longer than corolla tube, with non-overlapping lobes; corolla lobes \pm equaling the tube; anthers 0.3–0.7 mm long.
 3. Flowers 5-merous; calyx and corolla lobes acute to acuminate; capsules elliptical-ovate, \pm thickened around the interstylar aperture, with 1 seed _____ **1. *C. salina***
 3. Flowers 4- and 5-merous; at least some calyx and corolla lobes in the same flower long-attenuate; capsules globose to slightly depressed, not thickened apically, with 1–4 seeds _____ **2. *C. howelliana***
1. Infrastaminal scales completely absent or represented by lateral, dentate wings.
 4. Flowers 4–5-merous; calyx and corolla lobes long acuminate; infrastaminal scales represented by lateral, dentate wings; withered corolla surrounding capsule in the lower half _____ **4. *C. suksdorfii***
 4. Flowers 5-merous; calyx and corolla lobes acute but not acuminate; infrastaminal scales completely absent; withered corolla completely enveloping the capsule or leaving only its top visible.
 5. Flowers short-pedicellate; corolla not saccate between the stamen attachments (if slightly saccate then with all the following characteristics); styles 1.2–3 mm long; anthers oblong to linear, 0.7–1.1 mm long; capsule completely enclosed by corolla (top not visible); seeds not visible through the corolla and pericarp, which are thicker, not semitransparent _____ **5. *C. californica***
 5. Flowers sessile or subsessile; corolla saccate between the stamen attachments; styles 0.5–1(–1.5) mm; anthers broadly-elliptic, 0.25–0.5 mm long; capsule not completely enclosed by corolla (at least the top of capsule is visible); seeds visible through the thin and semitransparent corolla and pericarp _____ **6. *C. occidentalis***

1. *Cuscuta salina* Engelm. in W.H. Brewer, S. Watson, & A. Gray, Bot. Calif. 1:536. 1876. *Grammica salina* (Engelm.) Taylor & MacBryde, Canad. J. Bot. 56:186. 1978. LECTOTYPE

(Yuncker 1932): U.S.A. UTAH: Rio Virgen, on *Suaeda*, saline soil, Nov 1885, *Remy s.n.* (MO, fragment NY). This was essentially a renaming at specific rank (as "*C. salina*, Engelm. n. sp.") of what Engelmann had earlier published as *C. subinclusa* var. *abbreviata* and *C. californica* var. *squamigera*—both varieties were cited in synonymy. Yuncker (1932) specifically referred to the MO specimen ("Remy, in the herbarium of the Missouri Botanical Garden") as the type of *C. salina*.

Stems slender, orange-yellow. **Inflorescences** umbellate cymose clusters; pedicels 0.5–2.5 mm long; bracts 1(–0), ovate-lanceolate to lanceolate. **Flowers** 5-merous, white, 2.5–5(–6.2) mm long; papillae present or absent in the corolla; laticifers conspicuous in the perianth, ovary and capsule. **Calyx** campanulate to narrow-campanulate, about as long as the corolla tube, divided ca. 1/2 the length, glossy yellow or brownish when dried, lobes ovate-lanceolate, acute to acuminate, ± unequal, not basally overlapping or slightly so. **Corolla** 2.4–4.8(–6) mm long; tube cylindrical-campanulate to campanulate, 1.2–2.5 mm long, lobes ovate-lanceolate, acute to acuminate, ca. as long as the tube, erect to spreading, sometimes basally overlapping. **Stamens** included or exerted, anthers elliptical, 0.3–0.7 mm long, filaments equaling to longer than anthers. **Pollen** 3(–4)-zonocolpate 19–22(–26) µm, polymorphic, subsphaerical to subprolate, rounded at poles, tectum perforatum, puncta, 0.3–0.5 µm in diameter, granulate (Fig. 2a). **Infrastaminal scales** oblong, short-fringed, rarely reduced to sparingly fringed ridges ca. 1/2–2/3 the corolla tube length. **Styles** distinct, 0.4–1 mm long; stigmas capitate, globose. **Capsules** elliptical-ovate, 2–3.6 × 1.4–2.1 mm, ± thickened around the interstylar aperture, indehiscent or irregularly dehiscent, surrounded or capped by the withered corolla. **Seeds** 1 per capsule, not visible through the persistent corolla and pericarp, 1.35–1.57 × 1.25–1.43 mm, ± dorsoventrally compressed, broadly elliptic to subround, hilum subterminal, subround, 0.11–0.14 × 0.7–0.11 mm, vascular scar linear, 0.02–0.05 mm, oblique; surface of seed coat epidermis alveolate when dried and papillate when hydrated, cells 30–40 µm in diameter. *n* = 14 (Beliz 1986); *2n* = 30 (Pazy & Plitmann 1995).

KEY TO VARIETIES OF *CUSCUTA SALINA*

1. Papillae present on pedicels, calyx and/or corolla; infrastaminal scales represented by narrow, sparingly fringed ridges _____ **1c. *C. salina* var. *papillata***
1. Papillae absent; infrastaminal scales narrowly oblong, few-toothed.
 2. Corolla 2–3.5 mm; inland salt flats _____ **1a. *C. salina* var. *salina***
 2. Corolla 3–4.8(–6) mm; coastal salt marshes, tidal flats _____ **1b. *C. salina* var. *major***

1a. *Cuscuta salina* var. *salina*. *Cuscuta subinclusa* var. *abbreviata* Engelm., Trans. Acad. Sci. St. Louis 1:500. 1859. TYPE: U.S.A. CALIFORNIA. [Solano Co.]: Mare Island in San Francisco Bay, on *Arthrocnemum*, *Wright s.n.* (HOLOTYPE: MO).

Cuscuta californica Hook. & Arn. var. *squamigera* Engelm., Trans. Acad. Sci. St. Louis 1:499. 1859. *Cuscuta salina* var. *squamigera* (Engelm.) Yuncker, Illinois Biol. Monogr. 6, pt. 2–3:71, fig. 126. 1921. *Cuscuta squamigera* (Engelm.) Piper, Contr. U.S. Natl. Herb. 11:455. 1906. TYPE: U.S.A. UTAH: Rio Virgen, on *Suaeda*, saline soil, Nov 1855, *J. Remy s.n.* (HOLOTYPE: P; ISOTYPE: MO, fragment NY). Engelmann's protologue specifically noted "*J. Remy!* in Hb. Mus. Paris." Yuncker (1921) described the type of var. *squamigera* as "Rio Virgen, (Remy in 1855, ... a fragment in the En-

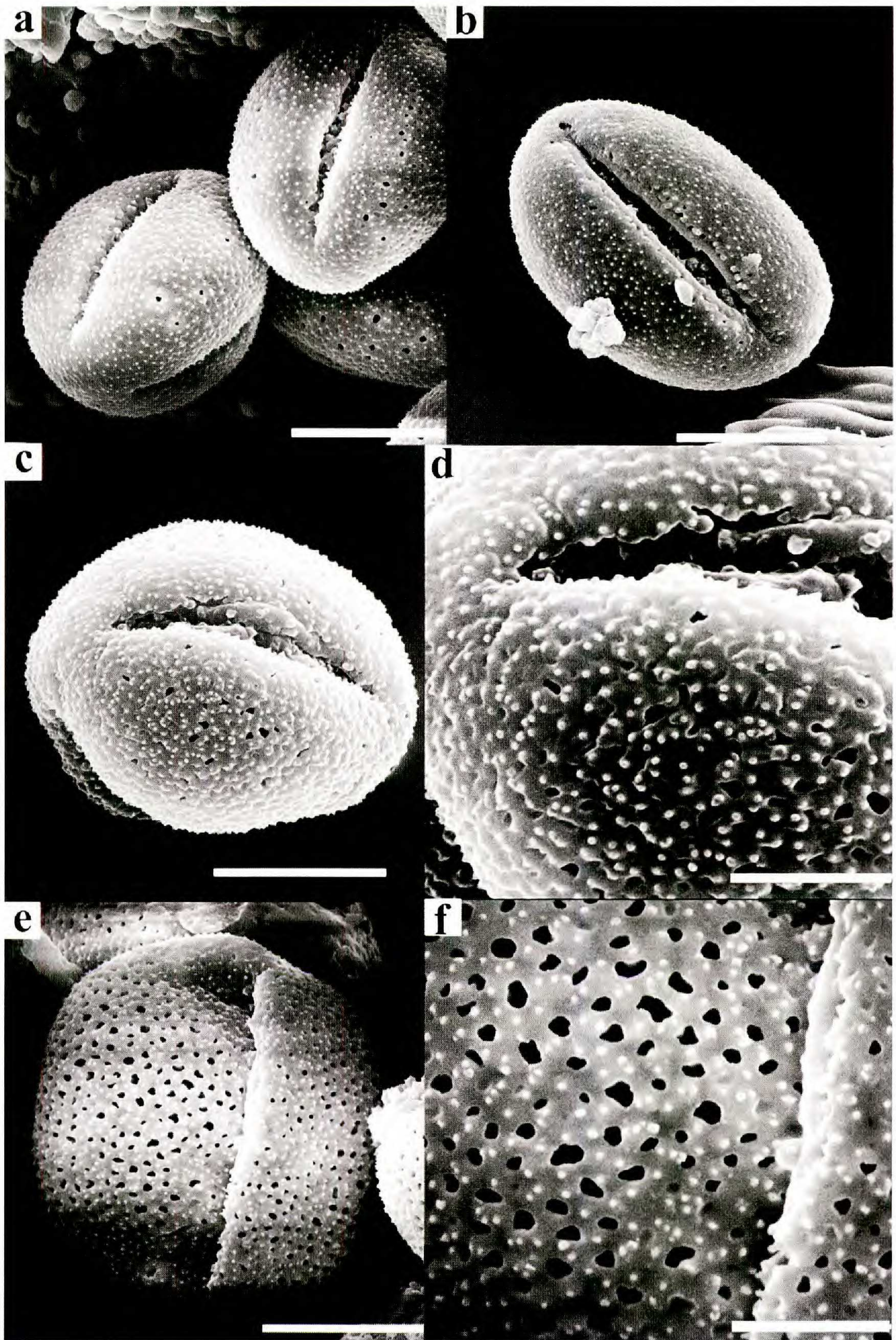


FIG. 2. Morphology of pollen. **a.** *Cuscuta salina* (scale bar = 10 μm). **b.** *C. occidentalis* (scale bar = 10 μm). **c.**–**d.** *C. howelliana* (scale bar = 10 and 3 μm , respectively). **e.**–**f.** *C. subinclusa* (scale bar = 10 and 3 μm , respectively).

gelmann Herb.).”

Distribution and ecology.—**CANADA:** British Columbia. **U.S.A.:** Arizona, California, Nevada, New Mexico, Oregon, Utah, Washington. **MEXICO:** Baja California. Flowering Apr–Nov. **Hosts:** *Atriplex*, *Cressa*, *Centromadia*, *Jaumea*, *Plantago*, *Salicornia*, *Salsola*, *Suaeda*, *Trichostema*, *Wislizenia*, in inland salt flats, marshes, ponds.

Conservation status.—T4 (apparently secure) (not yet assessed by NatureServe 2005).

1b. *Cuscuta salina* var. *major* Yuncker, Illinois Biol. Monogr. 6:161. 1921. TYPE: U.S.A. CALIFORNIA. Santa Clara Co.: Palo Alto, frequent on *Salicornia* in the marshes, 14 Sep 1901, *Baker 41* (HOLOTYPE: NY; ISOTYPES: CAS, GH, RSA).

Distribution and ecology.—**CANADA:** British Columbia. **U.S.A.:** California, Oregon, Washington. Flowering Jul–Oct. **Hosts:** various species, especially *Salicornia*, in coastal salt marshes, tidal flats.

Conservation status.—T3T4 (vulnerable to apparently secure) (not yet assessed by NatureServe 2005).

1c. *Cuscuta salina* var. *papillata* Yuncker, Bull. Torrey Bot. Club 69: 543. 1942. TYPE: U.S.A. CALIFORNIA. Mendocino Co.: Fort Bragg, 8–16 Aug 1912, *Eastwood 1593* (HOLOTYPE: GH, fragment NY).

Distribution and ecology.—**U.S.A.:** Arizona, California, Utah. Flowering Jun–Oct. **Hosts:** various species in salt marshes, flats, ponds.

Conservation status.—T3T4 (vulnerable to apparently secure) (not yet assessed by NatureServe 2005).

2. *Cuscuta howelliana* Rubtzoff, Leafl. W. Bot. 10:335. 1966. TYPE: U.S.A. CALIFORNIA. Lake Co.: Boggs Lake, open dry margin of the lake, inundated in winter, 20 Aug 1966, *Rubtzoff & Arnaud 5792* (HOLOTYPE: CAS, ISOTYPES: CAS, GH, OSC, RSA, UC).

Stems slender, yellow to orange. **Inflorescences** few- to many-flowered \pm glomerulate cymes, pedicels 0–0.6 mm long; bracts 1–0, lanceolate. **Flowers** embedded in the inflorescence of the host, 4–5-merous, 3–4.5 mm long, whitish, papillate-glandular. **Papillae** present in the calyx and corolla; elongated laticifers present in the calyx and corolla but not obvious (Fig. 1f). **Calyx** campanulate, ca. equaling corolla tube or exceeding it, divided 1/2–2/3 to the base, lobes unequal, triangular-ovate, acute, acuminate to long-attenuate and recurved at the apex, non-overlapping. **Corolla** tube cylindrical-campanulate, later more or less urceolate, ca. 1.5–2.2 mm long, lobes unequal, ca. equaling the tube, triangular-ovate, with acute to long-attenuate, recurved tips, suberect to spreading. **Stamens** included, anthers elliptical, 0.4–0.7 mm long; filaments 0.1–0.4 mm long. **Pollen** 3(–4)-zonocolpate (15–)17–22(–24) μm , polymorph, sphaerical to subprolate (subsphaerical more common), rounded at poles, tectum perforatum to microreticulate, puncta, 0.4–0.8 μm in diameter, granulate (Fig. 2 c, d).

Infrastaminal scales oblong-ovate, fringed, reaching to about the middle of the corolla tube; **Styles** distinct, evenly filiform, 0.4–1.1 mm; stigmas capitate, globose. **Capsules** globose to slightly depressed, 1.2–1.5 × 0.8–1.2 mm, not thickened apically, indehiscent or irregularly dehiscent, completely enclosed by the withered corolla and latter capped by it. **Seeds** 1–4 per capsule visible through the semi-transparent corolla and pericarp, 0.9–1.43 × 0.8–1.3 mm, dorsoventrally compressed to slightly angled, subround to broadly-elliptic, hilum subterminal, scar area clearly differentiated from the rest of the seed, broadly elliptic 0.21–0.25 × 0.12–0.15 mm, hilum linear 0.05–0.06 mm, vertical; heterogeneous; some areas are alveolate with cells 35–50 µm in diameter; some areas irregularly wrinkled (Fig. 3 c, e, f, g). **2n** = 26 (Beliz 1986).

Distribution and ecology.—**U.S.A.:** Endemic in California. Flowering Aug–Sep. **Hosts:** mostly *Eryngium aristulatum*, *E. vaseyi*, *E. castrense*, *E. alismaefolium*, *Navarretia leucocephala*, and *N. minima*, but also on *Polygonum kelloggii*, *Epilobium pygmaeum*; margins of vernal pools.

Conservation status.—G2G3 (imperiled to vulnerable) (G3, NatureServe 2005).

The biology of this species deserves future study. The parasite becomes strictly localized to the inflorescence region of the host. Flowers of *C. howelliana* develop inside the dense host inflorescences and apparently synchronize their anthesis with that of the host's flowers. The parasite achieves both protection and proximity to the flux of assimilates intended for the development of host's reproductive structures.

3. *Cuscuta subinclusa* Durand & Hilgard, J. Acad. Nat. Sci. Philad. ser. 2, 3:42. 1855. TYPE: U.S.A. CALIFORNIA. [Los Angeles Co.]: Tejon Pass, on a willow, *Heermann s.n.* (HOLOTYPE: PH presumably, fragment MO).

Cuscuta ceanothi Behr, Proc. Calif. Acad. (ed. 2) 1:16. 1854. The protologue gave no information regarding a type, and a neotypification probably will be required to firmly establish the identity of this name (see comments above). *Cuscuta ceanothi* is the earlier name but is tentatively placed here with *C. subinclusa*.

Stems medium, sometimes fleshy, creamy. **Inflorescences** few- to several-flowered, in scattered to densely aggregated clusters; pedicels 0–1 mm long; bracts 1–0, ovate to lanceolate. **Flowers** 5-merous, 5–7(–9 mm) long, white. Papillae present in the corolla lobes; laticifers isolated or in rows obvious in the calyx, corolla and fruit. **Calyx** campanulate, ca. 1/2 as long as the corolla tube, divided 3/5–2/3 the length, lobes broadly ovate to lanceolate, acute, sometimes cuspidate, basally overlapping. **Corolla** tube cylindrical, 2.5–3.5(–4.5) mm long, usually showing horizontal ridges between the stamen attachments when dry, lobes ovate-triangular, acute and often slightly acuminate, 1/4–1/3 as long as the tube, widely spreading to reflexed. **Stamens** subincluded; anthers linear 0.8–2 mm; filaments 0–0.1 mm. **Pollen** 3(–4)-zonocolpate (15–)17–22(–24) µm long, polymorph, subsphaerical to subprolate, rounded at poles, tectum microreticulate,

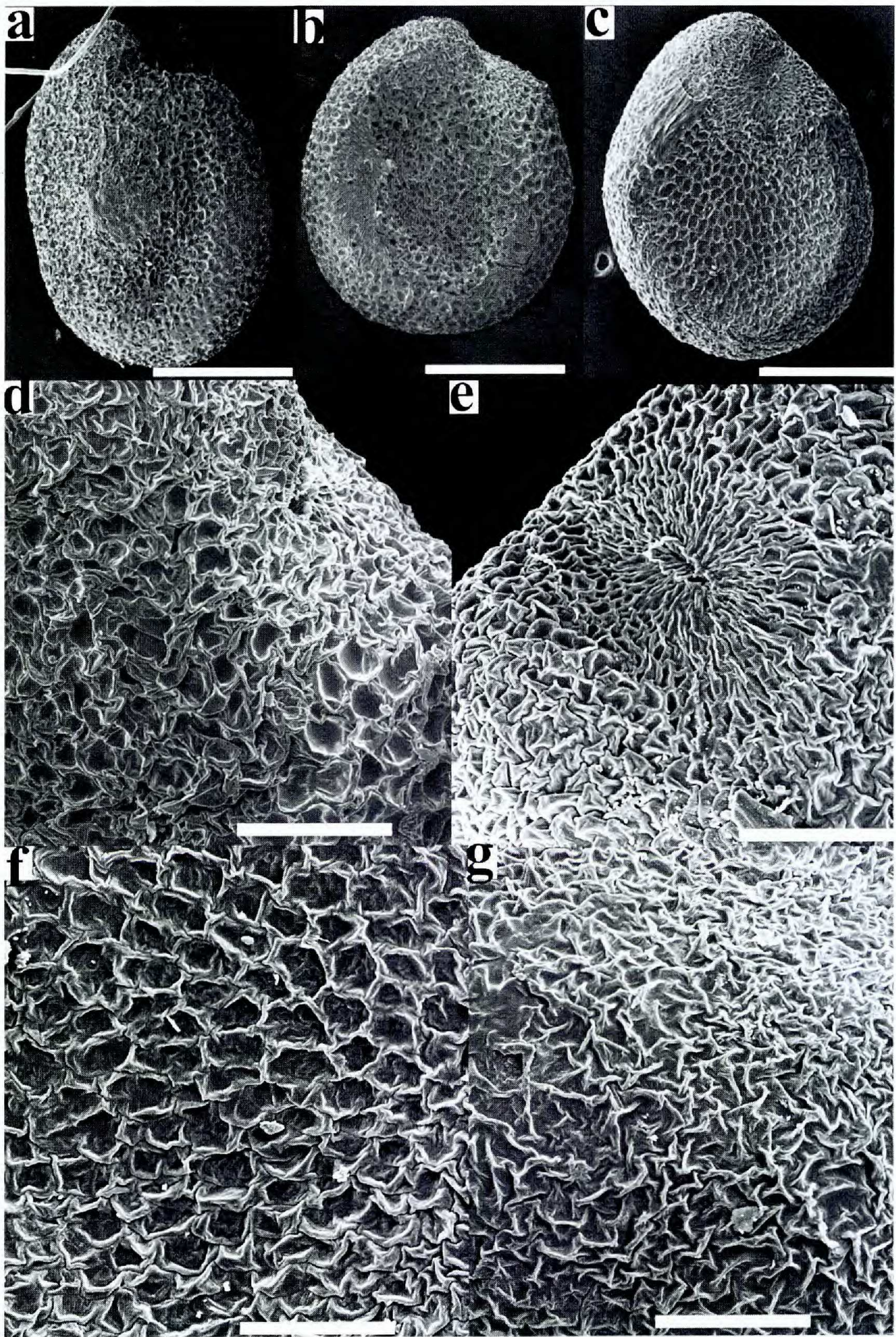


FIG. 3. Morphology of seeds. **a.** *C. californica* (var. *californica*), lateral view. **b.** *C. occidentalis*, lateral view. **c.** *C. howelliana*, lateral view (scale bar = 0.38 mm). **d.** Hilum of *C. californica*. **e–g.** *C. howelliana*: **e.** hilum, **f–g.** variation of seed coat micromorphology (scale bar = 100 μ m).

puncta, 0.4–0.9 μm in diameter, granulate (Fig. 2 e,f). **Infrastaminal scales** oblong to spatulate, irregularly short-fimbriate, ca. 1/2 as long as the corolla tube; styles 1–1.5 mm long; stigmas capitate, globose. **Capsules** ovate to elliptical, 1.5–3 \times 1.2–2.5 mm, pointed, thickened in the form of a collar about the interstylar aperture, indehiscent or irregularly dehiscent, capped by the withered corolla. **Seeds** mostly 1 per capsule, not visible through the capsule, subglobose to broadly ovoid, rarely slightly dorsoventrally compressed, 1.3–1.7 \times 1.2–1.5 mm; hilum terminal; seed coat cells alveolate/papillate when dried and papillate when hydrated, cells 30–40 μm in diameter. $n = 14$ (Beliz 1986).

Distribution and ecology—**U.S.A.**: California, Oregon. **MEXICO**: Baja California. Flowering Apr–Oct. **Hosts**: wide variety of woody and sometimes herbaceous plants growing along river banks and canyon bottoms, sometimes in salt marshes and deserts, including species of *Adenostoma*, *Amelanchier*, *Arcostaphylos*, *Artemisia*, *Asclepias*, *Ceanothus*, *Cercis*, *Citrus*, *Clematis*, *Erigeron*, *Grindelia*, *Heteromeles*, *Monardella*, *Rhus*, *Schinus*, *Populus*, *Rhododendron*, *Rosa*, *Salix*, *Solidago*, *Vitis*, particularly common on *Rhus* and *Eriogonum*.

Conservation status.—G4 (apparently secure) (not yet assessed by NatureServe 2005).

4. *Cuscuta suksdorfii* Yuncker, Mem. Torrey Bot. Club 18:167. 1932. TYPE: U.S.A. WASHINGTON. Skamania Co.: on an island of a mountain lake, on *Aster*, 24 Sep 1891, *Suksdorf 1487* (HOLOTYPE: US, fragment NY; ISOTYPES: GH, NY-2 sheets). This was essentially a renaming at varietal rank of *Cuscuta salina* var. *acuminata* (see below), but apparently Yuncker intended for it to be taken as a homotypic new species.

Stems slender, yellow. **Inflorescences** few-flowered umbellate clusters; pedicels 0–2 mm long; bracts 0–1, ovate lanceolate. **Flowers** 4–5-merous, white, 2.8–3.3 mm long; papillae absent; laticifers isolated in the calyx, corolla and ovary/capsule. **Calyx** broadly campanulate often zygomorphic, reaching ca 1/2 to the corolla lobes tips, divided 1/2–3/5, lobes ovate more or less unequal, with long-attenuate tips, not basally overlapping (Fig. 1e). Corolla 2.9–3.2 mm long; tube campanulate, 1.2–1.5 mm, lobes triangular-ovate, with lanceolate-attenuate tips, longer than the tube, suberect. **Stamens** included or barely visible through the corolla sinuses, anthers broadly elliptic, 0.2–0.4 mm long, filaments longer than anthers. **Pollen** 3(–4)-zonocolpate 18–22(–24) μm , polymorph, subsphaerical to subprolate, rounded at poles, tectum perforatum, puncta, 0.3–0.5 μm in diameter, granulate. **Infrastaminal scales** oblong, represented by shallowly toothed wings, 1/2–3/4 as long as the corolla tube; styles distinct, terete to slightly subulate, 0.3–0.7 mm long; stigmas capitate, globose. **Capsules** elliptical-ovoid, ovoid-conic, globose to depressed globose, 2–3.2 \times 2–3.6 mm, irregularly dehiscent, with withered corolla surrounding lower half. **Seeds** 2–4 per capsule, 0.80–1.1 \times 0.8–1.02 mm, dorsoventrally compressed, subround, hilum subterminal, 0.25–0.3 \times 0.2–0.28 mm, vascular scar, 0.04–0.07 mm, oblique; alveolate when dry and papillose when hydrated, cells 30–50 μm in diameter. $n = 14$ (Beliz 1986).

KEY TO VARIETIES OF *CUSCUTA SUKSDORFII*

1. Flowers on pedicels 0.5–2 mm; calyx 2.2–2.6 mm long; capsule globose to ovoid-conic _____ **4a. *C. suksdorfii* var. *suksdorfii***
1. Flowers sessile or subsessile; calyx 1.6–2 mm long; capsule globose to depressed globose _____ **4b. *C. suksdorfii* var. *subpedicellata***

4a. *Cuscuta suksdorfii* var. *suksdorfii*. *Cuscuta salina* var. *acuminata* Yuncker, Illinois Biol. Monogr. 6, pt. 2, 3:72, fig. 32, 89. 1921 (non *C. acuminata* Nutt. ex Engelm. 1859, in adnot.). TYPE: U.S.A. WASHINGTON. Skamania Co.: on an island of a mountain lake, 24 Sep 1891, *Suksdorf* 1487 (HOLOTYPE: US, fragment NY; ISOTYPES: CAS, GH, MO, NY-2 sheets).

Distribution and ecology.—**U.S.A.:** California, Oregon, Washington. Flowering Jul–Sep. **Hosts:** herbaceous species, mostly Asteraceae, *Calyptridium*, *Trifolium*. Mountain meadows, 5000–8500 ft.

Conservation status.—G2G3 (imperiled to vulnerable) (the same assessment in NatureServe 2005).

4b. *Cuscuta suksdorfii* var. *subpedicellata*. *Cuscuta suksdorfii* var. *subpedicellata* Yuncker, Bull. Torrey Bot. Club 62:512. 1935. TYPE: U.S.A. CALIFORNIA. Siskiyou Co.: Siskiyou Mts., Head E Fork Horse Creek, 6500 ft, S9 T47 N, R10 W, host: *Calyptridium umbellatum*, 21 Aug 1934, L.C. Wheeler 3192 (HOLOTYPE: NY).

Distribution and ecology.—**U.S.A.:** California, Flowering Jul–Sep. **Hosts:** *Calyptridium*. Mountain meadows, 6500 ft.

Conservation status.—G2G3 (imperiled to vulnerable) (the same assessment in NatureServe 2005).

5. *Cuscuta californica* Hook. & Arn., Bot. Beechey Voy., 364. 1839 (non Choisy 1842). TYPE: Presumably in K, not designated by Hooker and Arnott. Engelm. (1859) commented that “Both [Choisy and Hooker & Arnott] described this plant from Douglas’s specimens under the same name and in the same year (1841).” De Candolle (Prodr. vol. 9, 1845, p. 457) cited “hab. Nov. Californiam ubi rep. Douglas! h. soc. hort. Lond. Hook. bot. Beech. suppl. p. 364.” Yuncker (1921, 1932) apparently repeated de Candolle’s citation, noting for the type “‘Nov. Californiam’ (*Douglas*). Not seen.”

Stems medium, yellow to orange. **Inflorescences** loose, cymose-paniculate clusters; pedicels (0.5)1–2.5(–3 mm); bracts lanceolate to ovate. **Flowers** 5-merous, white, 3–5(–6.5) mm long; papillae sometimes present on the pedicels, receptacle, calyx and corolla; laticifers isolated, elongated present in the corolla and capsules. **Calyx** turbinate-campanulate, sometimes together with the receptacle, fleshy at the base, 1/2 to ca. as long as the corolla tube, divided 1/2–1/3 to the base, lobes triangular to lanceolate, acute to acuminate, basally overlapping. **Corolla** persistent; tube campanulate-cylindric, 1.9–2.7 mm, sometimes showing horizontal ridges between the stamen attachments when dry, rarely somewhat saccate, lobes narrowly lanceolate, acute, shorter than, equaling or longer than the tube, initially erect, later reflexed (Fig. 1 a, b, c). **Stamens** ± exerted when flowers are completely open, anthers oblong to linear, 0.7–1.1 mm long, filaments 0.1–1.1 mm long. **Pollen** 3(–4)-zonocolpate (16–)17.5–22.6(–26) μm, polymorph, spherical to pro-

late (the latter more common), rounded at poles, tectum imperforatum or with a few puncta, 0.2–0.3 μm in diameter, granulate. **Infrastaminal scales** completely lacking or reduced, 0.1 mm long at the base of the corolla tube. **Styles** distinct, evenly filiform, 1.2–3 mm long, stigmas capitate, globose. **Capsules** globose or ovoid-conic, 1.6–2.3 \times 1.8–2.5 mm, sometimes apically pointed, indehiscent or irregularly dehiscent, completely hidden by the withered corolla (Fig. 1g); pericarp and persistent corolla not semi-transparent (thicker than in *C. occidentalis*). **Seeds** 1–4 per capsule, not visible through the persistent corolla and pericarp, 0.90–1.4 \times 0.85–1.2 mm, dorsoventrally compressed, broadly-elliptic to obovate, hilum lateral, inconspicuous, subround 0.10–0.15 mm, vascular scar 0.05–0.06 mm, vertical; entirely alveolate (hilum area included) when dry and papillose when hydrated, cells 25–50 μm in diameter (Fig. 3a, d). $n = 14$ (Beliz 1986).

In some plants of *Cuscuta californica* (particularly of vars. *apodanthera* and *apiculata*), the receptacle and perianth cells located at the base of capsules and seeds are fleshy and become mucilaginous when brought in contact with water. A similar phenomenon occurs in *C. nevadensis* I.M. Johnston and to a lesser extent in *C. veatchii* Brandege; Costea et al. 2005 suggest these features may be related to vivipary observed in *C. nevadensis*. The fleshy receptacle and perianth base in *C. californica* may be homologous with those of *C. nevadensis*, but in contrast to *C. nevadensis*, *C. californica* does not have seeds with a globular-enlarged embryo at the hilum end. Apart from scattered observations such as these, the reproductive biology of *Cuscuta* species is poorly known (reviewed by Dawson et al. 1994; Costea & Tardif 2006).

KEY TO VARIETIES OF *CUSCUTA CALIFORNICA*

1. Ovary and fruit conic, apically pointed; 1-seeded _____ **5b. *C. californica* var. *apiculata***
1. Ovary and fruit globose to globose depressed; (1–)2–4 seeded.
 2. Flowers and pedicels densely papillate _____ **5c. *C. californica* var. *papillosa***
 2. Flowers and pedicels not papillate.
 3. Anthers sessile or subsessile _____ **5d. *C. californica* var. *apodanthera***
 3. Anthers not sessile, filaments shorter to equaling anthers _____ **5a. *C. californica* var. *californica***

5a. *Cuscuta californica* var. *californica*. *Cuscuta californica* Hook. & Arn. var. *graciliflora* Engelm., Trans. Acad. Sci. St. Louis 1:499. 1859. LECTOTYPE (designated here): U.S.A. CALIFORNIA: "Almost without flowers, on *Monarda*," Fremont's Expedition to California [without other data], 1846 (MO!). Engelmann cited "California, Douglas! Fremont! 506; Bigelow!"

Cuscuta californica Hook. & Arn. var. *longiloba* Engelm., Trans. Acad. Sci. St. Louis 1:499. 1859. LECTOTYPE (designated here): U.S.A. CALIFORNIA: San Felipe, on *Eriogonum polifolium*, Jan 1852, Thurber 633 (MO). Engelmann cited "Sta. Barbara, Nuttall! San Diego, Thurber! 570 & 633; Newberry!" Engelmann's material (at MO) of the Nuttall collection apparently is a fragment of the original specimen at PH, judging from notes inside the packet.

Cuscuta californica Hook. & Arn. var. *brachycalyx* Yuncker, Illinois Biol. Monogr. 6, nos. 2, 3:62, fig. 45, 75. 1921. TYPE: U.S.A. CALIFORNIA: Near Hanford, dry soil on *Centromadia pungens*, 21 Jun 1901, Kearney 52 (HOLOTYPE: NY; ISOTYPE: US).

Cuscuta brachycalyx Yuncker, Mem. Torrey Bot. Club 18:159. 1932. TYPE: U.S.A. CALIFORNIA: Near Hanford, dry soil on *Centromadia pungens*, 21 Jun 1901, Kearney 52 (HOLOTYPE: US). Yuncker treated this as a new species, even though he cited *C. californica* var. *brachycalyx* in synonymy.

Distribution and ecology.—**U.S.A.**: Arizona, California, Nevada, Oregon, Utah, Washington; **Mexico** (Baja California). Flowering Mar–Aug(–Sep). **Hosts**: *Abronia*, *Adenostoma*, *Agastache*, *Ambrosia*, *Asclepias*, *Convolvulus*, *Corethrogyne*, *Croton*, *Eriodictyon*, *Eriogonum*, *Holocarpha*, *Iva*, *Lupinus*, *Salvia*, and others. 200–22650 feet.

Conservation status.—T5 (common) (the same assessment in NatureServe 2005).

5b. *Cuscuta californica* var. *apiculata* Engelm., Trans. Acad. Sci. St. Louis 1:499. 1859. TYPE: U.S.A. CALIFORNIA: “Dry arroyos, on *Dalea spinosa*, [on the] Colorado,” 22 Feb 1884, J.M. Bigelow s.n. (HOLOTYPE: MO; ISOTYPES: GH, NY).

Distribution and ecology.—**U.S.A.**: California, Nevada. **MEXICO**: Baja California. Flowering Mar–Aug. **Hosts**: various species in sandy desert areas.

Conservation status.—T1T2 (critically imperiled to imperiled), (T3?, NatureServe 2005).

5c. *Cuscuta californica* var. *papillosa* Yuncker, Illinois Biol. Monogr. 6:152. 1921. TYPE: U.S.A. CALIFORNIA. San Bernardino Co.: San Bernardino Valley, Parish 5524 (HOLOTYPE: RM).

Distribution and ecology.—**U.S.A.**: California (endemic): Imperial, Riverside, San Bernadino, and San Diego cos. Flowering Mar–Aug, –Sep. **Hosts**: various species in sandy desert areas. 300–4600 feet.

Conservation status.—T3 (vulnerable) (the same assessment in NatureServe 2005).

5d. *Cuscuta californica* var. *apodanthera* Yuncker, Illinois Biol. Monogr. 6:152. 1921. *Cuscuta brachycalyx* var. *apodanthera* (Yuncker) Yuncker, Mem. Torrey Bot. Club 18:159. 1932. TYPE: U.S.A. CALIFORNIA: Yosemite Valley, 7–12 Jul 1896, Jepson 80a (HOLOTYPE: JEPS, fragment NY).

Distribution and ecology.—**U.S.A.**: Endemic in California. Flowering Aug–Sep. **Hosts**: *Eriogonum* and other herbs.

Conservation status.—T1T2 (critically imperiled to imperiled) (T2, NatureServe 2005).

6. *Cuscuta occidentalis* Millsp. [nom. nov.], Publ. Field Columbian Mus., Bot. Ser. 5:204. 1923. Based on *Cuscuta californica* Hook. & Arn. var. *breviflora* Engelm., Trans. Acad. Sci. St. Louis 1:499. 1859. *Grammica occidentalis* (Millsp.) Hadac & Chrtek, Folia Geobot. Phytotax. 8:220. (Aug) 1973. *Grammica occidentalis* (Millsp.) W.A. Weber, Southw. Naturalist 18:319. (Oct) 1973. TYPE: U.S.A. CALIFORNIA. Monterey Co.: Monterey, in fields, [no date], Hartweg 1863 (HOLOTYPE: MO; ISOTYPES: GH, NY).

Stems medium, yellowish to orange. **Inflorescences** compact glomerulate clusters; pedicels 0–0.5(–1.5 mm); bracts lanceolate to ovate. **Flowers** 5-merous, white

to creamy; 2.7–3.4 mm long; papillae rarely present; laticifers not conspicuous (Fig. 1d). **Calyx** campanulate, somewhat shorter to ca. as long as the corolla tube, divided 2/5–1/2 the length, rarely fleshy at base, lobes narrowly ovate to lanceolate, acuminate, not basally overlapping; corolla tube cylindrical-campanulate, 1.4–2.1 mm long, saccate between the stamen attachments, lobes lanceolate, acuminate, shorter than the tube, initially erect, later usually spreading (sometimes reflexed) giving flowers a star-shaped appearance. **Stamens** ± exerted; anthers broadly-elliptic, 0.25–0.5 mm long, filaments 0.3–1 mm long. **Pollen** as in *C. californica*, (17–)19–24(–26) µm long. **Infrastaminal scales** as in *C. californica*; styles distinct, evenly filiform, styles 0.5–1(–1.5) mm long; stigmas capitate, globose. **Capsules** globose to globose-depressed, 1.8–2.2 × 2–2.6 mm, indehiscent or irregularly dehiscent, not completely enclosed by the corolla (the top of capsule visible) (Fig. 1h); corolla and pericarp thin, membranous and semi-transparent. **Seeds** 2–4 per capsule, visible through both corolla and pericarp, 0.85–1.3 × 0.8–1.1, dorsoventrally compressed, subround to broadly-elliptic, hilum subterminal, poorly differentiated from the rest of the seed, subround 0.10–0.15 mm, vascular scar 0.05–0.06 mm, vertical, surface of seed coat alveolate when dry (including hilum area), cells 25–50 µm in diameter (Fig. 3b).

Distribution and ecology.—**U.S.A.:** California, Colorado, Idaho, Nevada, Oregon, Utah, Washington, Wyoming. **MEXICO:** Baja California. Flowering Mar–Aug(–Sep). **Hosts:** *Artemisia*, *Boisduvalia*, *Calyptridium*, *Corethrogyne*, *Ericameria*, *Eriogonum*, *Hemizonia*, *Iva*, *Lotus*, *Lupinus*, *Monardella*, *Oenothera*, *Polygonum*, *Salvia*, *Sisymbrium*, and others. 25–6500 feet.

Conservation status.—G4G5 (apparently secure to secure) (not assessed yet by NatureServe 2005).

APPENDIX 1.—VOUCHERS FOR THE SEM STUDY

Vouchers are from NY unless otherwise indicated.

1. ***Cuscuta salina*** (see Costea et al. 2005).

2. ***Cuscuta howelliana*** (7 collections examined).—**U.S.A. CALIFORNIA. Butte Co.:** ca 7 mi N of Oroville, N Table Mountain, E side of Cherokee Rd., 1325 ft, 18 Jul 1998, *Ahart 8044* (JEPS). **Sacramento Co.:** ca 1 mi S of White Rock Rd. and Scott Rd. intersection, 27 May 1985, *Bowcutt 331* (UC). **Shasta Co.:** between Goose Valley and Burney Valley, ca. 3.5 mi NNW from Burney, 3200 ft, 8 Aug 1988, *Taylor 10026* (JEPS). **Siskiyou Co.:** 16 mi N of Fall River Mills (Shasta Co.) and 6 mi W of Day (Modoc Co.), 1.2 mi E of Spring Creek Rd., 3600 ft, 19 Jul 1989, *Powell 3533* (JEPS). **Tehama Co.:** ca 10 mi SE of Corning, S Fork Hall Creek, 460 ft, 12 May 1995, *Taylor 14897* (JEPS); BLM parcel along Hwy 36 NE of Red Bluff, 870 ft, 8 Jul 1996, *Oswald & Ahart 7978* (JEPS); Inks Creek, ca. 1.5 mi N of Dales Lake, 612 ft, 27 May 1992, *Taylor 12661* (UC).

3. ***Cuscuta subinclusa*** (11 collections examined).—**U.S.A. CALIFORNIA.** [no county given, **Los Angeles or San Bernardino Co.?**] Swartout, 1 Sep 1939, *Grace s.n.* **Los Angeles Co.:** Liebre Mts., entrance to Ruby Canyon of Forest Service Rd., ca. 1/10 mi from junction with Lake Hughes Rd., 2000 ft, 23 Oct 1996, *Raz & Boyd 015*; Lower Spunky Canyon, stretch draining SSE exiting into Bouquet Reservoir, 2995–3065 ft, 20 Sep 1994, *Ross & Boyd 8260*; San Gabriel Mts., Tujunga Creek,

near mouth of Canyon, 23 Aug 1937, *Ewan 11049*. **Marin Co.:** mouth of San Antonio Creek, 3 Sep 1939, *Howell 15355*; Mouth of San Gabriel Canyon, 17 Dec 1935, *Hastings s.n.*; San Antonio Slough, N of Novato, 5 ft, 3 Sep 1939, *Rose 39363*. **Monterey Co.:** Banks of San Antonio River, Santa Lucia Mts., 25 Oct 1930, *Mason 5766*. **Nevada Co.:** Banner Mt., ca. 4 mi E of Nevada City, 3900 ft, 15 Jul 1965, *True & Howell 2315*. **Plumas Co.:** Mill Creek, Jun 1877, *Austin s.n.* **San Joaquin Co.:** San Joaquin Bridge near Lathrop, 9 Sep 1892, *Brandege s.n.*

4. *Cuscuta suksdorfii* (5 collections examined).—**U.S.A. CALIFORNIA. Humboldt Co.:** Trinity Summit, near Box Camp, 5000 ft, 4 Aug 1949, *Tracy 18430* (UC). **Siskiyou Co.:** Siskiyou Mts., Mt. Diablo, 1 mi E Dry Lake Lookout, 6000 ft, 31 Jul 1934, *Wheeler 3011* (JEPS); [**Co. unspecified**] Kings Canyon National Park, Woods Creek, near base of Castle Dome, 8500 ft, 27 Jul 1948, *Bailey & Bailey 2672a* (UC). [**Co. unspecified**] ca 1/4 mi E of Yuba Gap and Hwy 80, E side of the paved road to Lake Valley Reservoir, 5840 m, 22 Jul 2002, *Ahart 9885* (JEPS). [No location, no date, no collector] (UC 23290).

5. *Cuscuta californica*.

5a. *Cuscuta californica* var. *californica* (13 collections examined).—**U.S.A. CALIFORNIA.** [locality illegible], 21 Jun 1931, *Yuncker & Welch 3748*. **Kern Co.:** "brachycalyx," 1.5 mi N of Kernville, 2670 ft, 28 Sep 1962, *Howell 38877*. **Los Angeles Co.:** Liebre Mts., Knapp Ranch at the upper end of Castaic Creek drainage in broad alluvial valley at head of Cienega Canyon, S of Liebre Mt., 2840–3080 ft, 28 May 1997, *Boyd 9839*; [some flowers "brachycalyx"-like] Whittier Hills, S-draining tributary of Turnbull Canyon, 980–1000 ft, 15 Jun 1992, *Ross 6575*; Mount Wilson, 3000 ft, 17 Jul 1931, *Yuncker & Welch 3704, 3707*. **Orange Co.:** Santa Ana Mts., Silverado Canyon, 21 Jun 1931, *Fosberg 5143*. **Riverside Co.:** 8 mi SE of Corona, along road to Elsinore, 17 Mar 1964, *Hitchcock & Muhlick 23076*. **San Bernardino Co.:** foot hills of San Bernardino Mountains, 15 Jun 1898, *Parish s.n.* **San Diego Co.:** Jamul Valley, Jun 1875, *Palmer 439*; San Diego, Mission Hills, 14(?) May 1903, *Abrams 3462*; along Hwy 78E 5.3 Mi W of Ramona, 15 Jun 1973, *LeDoux et al. 114*; [some flowers "brachycalyx"-like] Coronado Beach, 24 Jun 1932, *Moldenke 7037*. **San Luis Obispo Co.:** Pismo, 25 Aug 1932, *Demaree 9281*. **NEVADA. Clark Co.:** Hells Kitchen area near Gold Butte, Devils Cove Rd., 2.9 mi S of Connolly Spring, 2400 ft, 14 May 1986, *Pinzl 7238a*.

5b. *Cuscuta californica* var. *papillosa* (5 collections examined).—**U.S.A. CALIFORNIA.** [no locality], Aug 1901, *Grant 4449*. **Riverside Co.:** Cathedral City, 23 Apr 1945, *Lillian s.n.*; ca. 500 ft, 27 Dec 1945, *Rose 45331*; Cathedral Canyon, 23 Dec 1946; *Rose 46300*. **San Bernardino Co.:** 1/2 mi E of Hawes Ranch, Horsethief Canyon, Mohave River tributary, 3300 ft, 17 Sep 1933, *Wheeler 2114*.

c. *Cuscuta californica* var. *apiculata* (3 collections examined).—**U.S.A. CALIFORNIA. Riverside Co.:** Cathedral City, no date (probably 1945), *Blake s.n.* **NEVADA. Clarke Co.:** 4 mi SE of Muddy Peak at head of Callville Wash, 2500 ft, 28 May 1937, *LaRivers & Hancock 261*; 29 May 1937, *LaRivers & Hancock 231*.

6. *Cuscuta occidentalis* (14 collections examined).—**U.S.A. CALIFORNIA. Fresno Co.:** Copper Creek Canyon Creek Trail, 7200 ft, 2 Aug 1958, *Howell 34198*. **Mono Co.:** 1 mi E of Mammoth Post Office, 29 Jul 1951, *Raven 3720*. **Monterey Co.:** Point Lobos State Park, 16 Jun 1935, *Lee & Mason 9219*. **Siskiyou Co.:** along Klamath River Hwy. W of Pacific Hwy., 2000 ft, 20 Jun 1940, *Yuncker 15144*. **Trinity Co.:** Cold Springs Area, South Fork Mt., 5400 ft, 28 Aug 1941, *Parks & Tracy 11517*. **Washoe Co.:** ca 1 mi ENE of Grass Valley Reservoir, 6000 ft, 14 Aug 1991, *Schoolcraft et al. 2220*. **COLORADO. Delta Co.:** Paonia, 23 Jul 1911, *Osterhout 4602*. **IDAHO. Adams Co.:** 2 Mi S of Council, 26 Aug 1937, *Christ & Ward 8787*. **Gooding Co.:** Little City of the Rocks in the Mt. Bennett Hills N of Gooding, 28 Jul 1976, *Ertter 2027*. **NEVADA. Douglas Co.:** Antelope Valley at the E edge of Red Hill on the E side of Gray Hills, 4990 ft, 14 Jul 1997, *Tiehm 12257*. **Eureka Co.:** Roberts Mts., 1.7 mi N of Three Bars Ranch on the main road to Tonkin Summit, 6600 ft, 22 Aug 2002, *Tiehm 14108*. **Mineral Co.:** E slope of Wassuk Range, base of Big Indian Mt., 9500 ft, 11 Sep 1938, *Archer 7032*. **Washoe Co.:** dry bed of Ice Pond, Whittell-Audubon Area, Carson Range foothills, 5480 ft, 12 Aug 1974, *Howell et al. 50745*. **UTAH. Salt Lake Co.:** [no locality], 16 Aug 1907, *Garrett 2170*.

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